



## Phytoplankton size changes and diversity loss in the southwestern Mediterranean Sea in relation to long-term hydrographic variability

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### ABSTRACT

Structural changes in plankton primary producers have large implications for food web dynamics, energy fluxes and the vertical export of biogenic particulate carbon. Here we examine phytoplankton data spanning the period 1993–2008 from the Bay of Tunis, southwestern Mediterranean Sea, in relation to long term hydroclimate variability. We show a conspicuous shift in the structure of the phytoplankton community characterized by an increase of small-sized species and diversity loss, revealing a dominance of smaller blooming diatoms and cyanobacteria. Such changes were concurrent with marked modifications in hydroclimatic patterns experienced in the Bay of Tunis consisting of a shift towards enhanced winter precipitation together with rising temperatures. This novel study shows an overall rise in the proportion of small phytoplankton cells and a decreasing trend in phytoplankton diversity in the southern Mediterranean area. These findings warn of a potential decline of trophic efficiency and lesser food web stability resulting from mean size reduction and the diversity loss.

### 1. Introduction

Understanding how climate variability influence the dynamics of marine communities is essential to cope with climate impacts into resources management risks under scenarios of global change. Marked ecological modifications fostered by climate warming, so far documented, include (i) changes in latitude/altitude species' ranges (Root et al., 2003), (ii) in the timing of seasonal ecological events in organism life-cycles, i.e. phenology (Edwards and Richardson, 2004), and (iii) a decrease in the mean body size of communities (Daufresne et al., 2009); the latter being considered the third universal response to warming (Peter and Sommer, 2013). Body size is a key ecological trait driving physiological processes, the dynamics of trophic interactions and energy fluxes in marine food webs. At the bottom of pelagic food webs, changes in dominant cells size further impact biogenic particulate carbon export towards the seabed, as larger phytoplankton cells sink faster than smaller ones. Hence, deciphering underlying causalities of size reduction in marine ecosystems is a current ecological challenge and a

pressing endeavor in a changing world ocean.

Temperature influences phytoplankton both directly, via physiology, and indirectly, through factors controlling nutrient availability. For instance, in temperate marine ecosystems, high temperature foster stratification, thereby shaping light and nutrients availability. Indeed, recent investigations based on meta-analysis of large data sets have pointed out a leading role of resource availability in the phytoplankton size structure (Marañón et al., 2015, 2012). Likewise, mesocosms experiments have shown that temperature effects on cell size are mainly mediated by nutrient limitation (Peter and Sommer, 2013). That is, by promoting a higher stratification, warming indirectly reduce nutrients supply and primary production in surface layers, which foster a decrease of large cells along with a decline in biogenic carbon export (Chust et al., 2012; Falkowski and Oliver, 2007). The relationship between temperature and resource supply is however not trivial. It varies among ecosystems as nutrient inputs are also affected by upwelling processes, riverine discharges or even human impact. Hence, underlying factors linking warming and phytoplankton size structure are case-specific, and

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therefore difficult to model (Marañón et al., 2015).

To date, a number of studies have documented a significant increase in the proportion of small-sized species concurrently with warmer conditions in a variety of systems, including freshwater (Daufresne et al., 2009), estuaries (Guinder et al., 2012) and marine ecosystems (Suikkanen et al., 2013). In the Mediterranean basin, research efforts have mainly focused on northern coasts, i.e. the Gulf of Naples (Ribera d'Alcalà et al., 2004), the central Adriatic (Mozetič et al., 2012) and the Ligurian Sea (Goffart et al., 2002; Marty et al., 2002), where phytoplankton responses to warming have shown structural changes unveiling a decline of larger cells in the community. In contrast, little is known on phytoplankton dynamics in southern coasts, although such areas may be more vulnerable to global anthropogenic changes due to the coastal concentration of anthropogenic activities due to the increasing of population density (IPCC, 2014). Furthermore, there is a lack of reports on phytoplankton variability covering recent years when Mediterranean surface waters have shown pronounced rising temperatures (Macias et al., 2013). Here, we compiled field data over the period 1993 to 2008 from a shallow ecosystem in the northern Tunisian coast, southwestern Mediterranean. We assessed hydroclimate trends, as shown by SST and precipitation, and their influence on the phytoplankton community structure, e.g. size, biomass, abundance and species shifts. We discussed on the impending consequences on phytoplankton size structure and diversity in highly productive neritic areas under projected warming scenarios in the Mediterranean Sea.

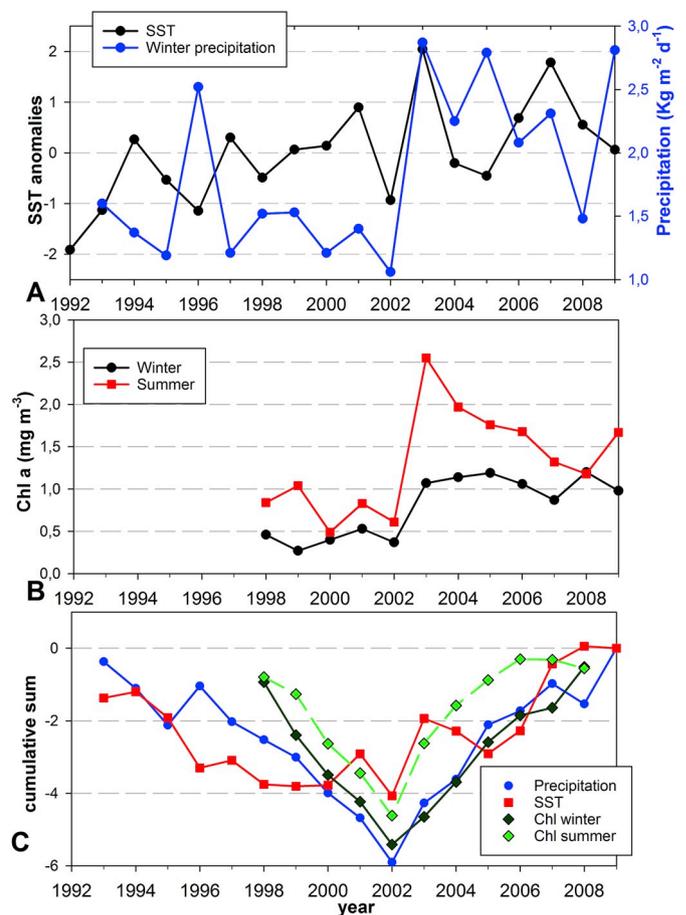
## 2. Methods

Hydrological features of the Bay of Tunis are influenced by the inflowing Atlantic waters in the northernmost part (Millot, 1999), whereas the southern area is characterized by shallow, eutrophic coastal lagoons (Supplementary Information SI Fig. 1) (Daly Yahia-Kéfi et al., 2005). The nutrient dynamics shows a zonal trophic gradient from the eutrophic southwestern region to the mesotrophic northeastern area (Souissi et al., 2000).

### 2.1. Biological data

Plankton samples were collected from the 5 m depth surface layer in two shallow stations at the most inner bay (36.76 N, 10.50 E; 36.80 N, 10.32 E), mainly with a monthly frequency over the period 1993 to 2008. The sampling was interrupted during the years 1996–1999, and there are also some gaps during 2005–2006 (SI Table I). At each sampling site, 1 L of seawater was collected using 2 L Ruttner bottle from the surface water (-0.5 m) for chemical analyses and for phytoplankton counting. Samples treatment over the whole period was done consistently by the same senior expert taxonomist (O. Kéfi - Daly Yahia). Samples were fixed by addition of formaldehyde and acid Lugol's solutions, considered at 0.4% and 3% final concentration, respectively. Subsequently, samples were stored in the dark at room temperature until analysis and for long term storage, samples were kept in cold place.

Phytoplankton cells from 25-ml subsamples were counted under an inverted microscope (Hund) using 200 and 400 magnifications (Utermöhl, 1958; Lars and Malte, 2010). Different counting methods were used to account for the diversity of the sample (Andersen and Thronsdén, 2004): (i) when species are characterized by low abundances, all species were counted by sweeping the entire sedimentation 25 mL chamber up and down and vice versa; (ii) one or more dominant species; cells were counted along two or more transverse lines using a counting grid placed in the eyepiece. Phytoplankton size fractionation for was done based on the longest axis of the cells following techniques, as described by Munawar and Munawar (1986). Phytoplankton size was examined on 30 to 50 individuals of each dominant species in the sample in order to ensure representativeness.



**Fig. 1.** A- SST yearly averaged anomalies (black dot) and winter precipitation (DJFM, blue dot) along the monitoring period.

B-Seasonally averaged chlorophyll time series for: winter (black dot, DJFM) and summer (red square, JJA).

C- Cumulative sums for different variables: SST (red square); precipitation (blue dots); chlorophyll winter (dark green diamond); chlorophyll summer (light green diamond). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

### 2.2. Physical data

We used regional climate data covering the period 1993–2009. Sea surface temperature (SST) relative to the Bay of Tunis was obtained from Copernicus Marine Environmental Monitoring Services (<http://marine.copernicus.eu/>). This Level-4 product is specific for the Mediterranean Sea and has a  $0.04 \times 0.04^\circ$  resolution (SST\_MED\_SST\_L4\_REP\_OBSERVATIONS\_010\_021) (Buongiorno Nardelli et al., 2013; Pisano et al., 2016). Precipitation rates relative to the Bay of Tunis were obtained from ERA5 climate reanalysis dataset, with  $0.25^\circ$  of horizontal resolution (Copernicus Climate Change Service, C3S, <https://doi.org/10.24381/cds.f17050d7>). We extracted monthly means of daily precipitation for the entire time series.

In addition, we used Chlorophyll a estimates from the inner Bay of Tunis derived from satellite, available from Copernicus Marine Environmental Monitoring Services (<http://marine.copernicus.eu/>). This Level-4 product is specific for the Mediterranean Sea and has a 1 Km resolution (OCEANCOLOUR\_MED\_CHL\_L4\_NRT\_OBSERVATIONS\_009\_041; Volpe et al., 2012); chlorophyll monthly means were extracted for the available period, 1998 to 2009.

### 2.3. Statistical analysis

Due to some gaps in the data series, and in order to use the longest

and most coherent temporal data, we pooled together phytoplankton data from the two sampled stations to show the interannual variations during winter (DJFM) and summer (JJA) (SI Table 1). The two stations are located in shallow areas (5 m, Fig. SI 1) and present a similar nutrient dynamics (Souissi et al., 2000).

SST series were seasonal detrended prior computing monthly anomalies and annual average means. Precipitation, which occurs mainly during winter season, was averaged using the same months as for phytoplankton winter variability (DJFM).

Periods with predominantly positive or negative anomalies were assessed by means of the cumulative sum method (cusum or cusum transformed). To do this, we standardized the time series to zero mean and unit variance, and then cumulate the standardized values over time. Each data point,  $y_t$ , corresponding to time  $t$  ( $t$  from 1 to  $n$ ) was added to the preceding data point according to the equation:

$$St = \sum_{t=1}^n yt \quad (1)$$

The interpretation is based on the slope of the line on chart. A constant deviation from the mean of the time series shows a constant slope. Persistent changes from the mean of the time series cause a persistent change of the slope. The cumulative sum enables us to detect in a simple way local changes and homogeneous periods in a time series (Ibanez et al., 1993).

In addition, we computed a driver-response plot using paired observations, on a monthly basis, with a potential driver (SST and precipitation) and the chlorophyll monthly anomalies as potential response. The observations were ordered following an ascending order of each of the driver variable and then the chlorophyll data was transformed in a cusum following equation (2). This method has been previously used to assess thresholds and underlying driver-response in complex environmental time series (Regier et al., 2019).

Diversity changes in the phytoplankton community were assessed by means of the Shannon Index ( $H'$ ) of phytoplankton community, following:

$$H' = -\sum_{i=1}^R (p_i * \ln p_i) \quad (2)$$

where  $p_i$  is the proportion of individuals belonging to a species  $i$  per sample and  $R$  the total number of species per sample. A heat map was used to display interannual variations of the ten most abundant species of phytoplankton, diatoms and cyanobacteria. To do so, data (cells  $L^{-1}$ ) were ranged and a specific color was assigned denoting low (blue) to high abundance values (yellow), respectively.

### 3. Results

The annual pattern of salinity displayed average values of  $36.34 \pm 2.61$ , with maximum reached 38–38.8 in August, while minimum values, approx. 26.6–27, were registered during rainy periods (from September to June). In turn, the annual pattern of SST showed an average of  $19.6 \text{ }^\circ\text{C} \pm 4.2$ , although during the last years of series (2005–2009) an upward trend was observed (Fig. 1 a, Table 1). Regional climate drivers in this shallow ecosystem, SST and winter precipitation (DJFM) showed statistical significant changes, as described by the cusum-transformed time series (Fig. 1 a,c) (Table 1). The cusum results displayed two main periods, statistically significant ( $t$ -test,  $p < 0.05$ ) characterized by low values during (1993–2002), followed by a shift towards higher values during the years 2003–2009.

Chlorophyll  $a$ , as a proxy of phytoplankton biomass, followed a seasonal cycle denoted by maxima during summer months in both aforementioned periods, before and after 2002. Minima were found during November–December approx.  $0.5 \text{ mg m}^{-3}$  and maxima during June–July approx.  $1.3 \text{ mg m}^{-3}$  (Fig. SI 2). This pattern following the

**Table 1**

Results of average anomalies before/after 2002 after cumulative sums (cusum) analysis (Fig. 1). All variables present before/after 2002 statistically significant differences,  $t$ -test,  $p < 0.05$ .

Average anomalies of climatic drivers		
Variable		Second period (2003–2009)
SST	First period (1993–2002)	0.581
Winter precipitation		0.843
Average anomalies of phytoplankton variables		
Variable		Second period (2003–2009)
Chlorophyll	First period (1993–2002)	0.773
	Winter	0.659
Phytoplankton cells	First period (1993–2002)	0.454
	Summer	0.587
Small phytoplankton cells	First period (1993–2002)	0.469
	Winter	0.641
Phytoplankton biodiversity Index $H'$	First period (1993–2002)	0.481
	Summer	0.565
Diatoms biodiversity Index $H'$	First period (1993–2002)	0.538
	Summer	0.452

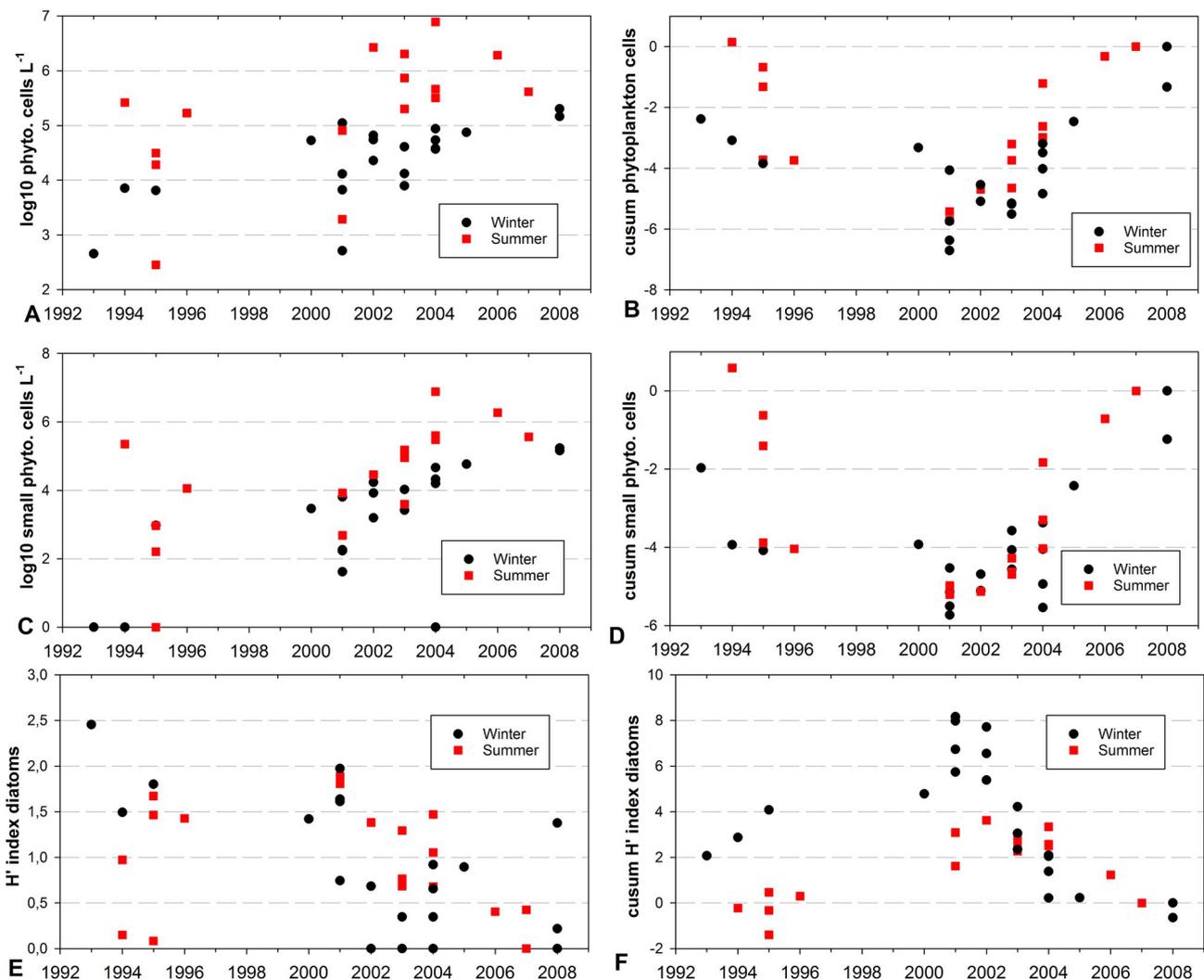
seasonal sunlight cycle suggests there is no nutrient limitations via stratification in this shallow ecosystem affected by anthropic nutrients loads from small rivers and coastal lagoons (Sommer et al., 2012). Regarding the interannual variability, both summer and winter chlorophyll data showed an upward shift since 2002 (Fig. 1 b,c; Table 1). Both trends are tightly correlated with winter precipitation, particularly summer chlorophyll values when maximum levels were registered (Fig. 1,c and Fig. SI 2 b). In addition, chlorophyll concentrations shifted from negative monthly anomalies to positive overcoming a precipitation threshold around  $2 \text{ kg m}^2 \text{ d}^{-1}$  (Fig. SI 4).

Phytoplankton abundance showed a marked intra-seasonal variability along with an overall upward shift since 2002, reaching approx. A higher order of magnitude at the end of the series, from  $10^4$  to  $10^5$  cells  $L^{-1}$  for winter values and finally reaching  $10^6$  cells  $L^{-1}$  during summers (Fig. 2 a,b). The abundance change was mainly driven by small cells (Fig. 2 b), as showed by the interannual variability of small phytoplankton (2–20  $\mu\text{m}$ , nanophytoplankton), which displayed a significant abundance increase from  $10^2$  to  $10^5$  cells  $L^{-1}$  during both seasons since 2002 (Fig. 2 c,d). Structural changes in the phytoplankton community were further evidenced in diversity, indexed by the Shannon Index ( $H'$ ). Phytoplankton and diatoms, the most dominant group presenting blooms here, showed both a pronounced loss of diversity in winters and summers (Fig. 2 e,f; Fig. SI 3).

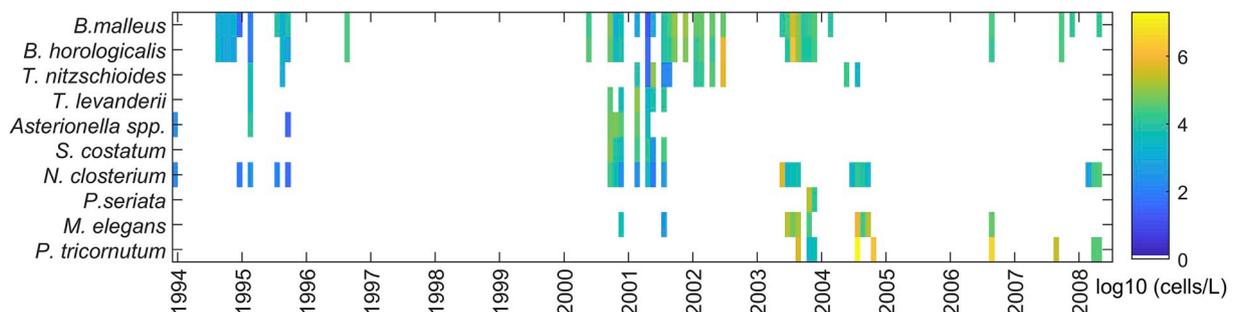
The ten most abundant species recorded throughout the investigated period are shown in Fig. 3. Coastal areas were mainly dominated by diatoms and showed the highest diversity over the years 1994–2002 (Fig. 2 b,d and 3). *Bellerochea horologica* and *Bellerochea malleus* were initially the most representative diatom species, reaching typical bloom abundances in 2001–2003 ( $10^6$  cells  $L^{-1}$ , Fig. 3 and Fig. SI 5) (Hallegraeff, 1993). Other species, such as *Thalassionema nitzschioides* showed a scattered pattern through the whole time series. We noticed, however, an increase of small diatoms, falling within nanoplankton sizes, since 2002 with blooms of *Nitzschia closterium* and *Phaeodactylum tricornutum*. Particularly, *P. tricornutum* presented high abundances reaching up to  $10^6$  cells  $L^{-1}$  (Fig. 3 and Fig. SI 5). To the best of our knowledge, this is the first time that such high field abundances have been reported for this diatom widely used in laboratory conditions. Furthermore in the last years, cyanobacteria reached marked peaks with *Merismopedia elegans* as the dominant species within this group (Fig. 3 and Fig. SI 5).

### 4. Discussion

We have investigated temporal changes in phytoplankton in the northern Tunisian coast. The analysis revealed structural changes in the phytoplankton community, which shifted towards a dominance of



**Fig. 2.** Phytoplankton time series pooled by summer months (red square, JJA) and winter (black dot, DJFM). Cells abundance ( $\log_{10}$  cells  $L^{-1}$ ) of total phytoplankton community and derived cusum transform (A,B); small cells (nanophytoplankton, 2–20  $\mu m$ ) and derived cusum transform (C,D). Biodiversity of diatoms, collected by the Shannon Index ( $H'$ ) and derived cusum transform (E,F). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)



**Fig. 3.** Cell abundances ( $\log_{10}$  cells  $L^{-1}$ ) for the ten most representative species along the time series: *Bellerochea malleus*; *Bellerochea horologicalis*; *Thalassionema nitzschioides*; *Thalassiosira levanderii*; *Asterionella* spp.; *Skeletonema costatum*; *Nitzschia closterium*; *Merismopedia elegans*; *Phaeodactylum tricornutum*.

smaller cells along with a loss of diversity.

#### 4.1. Hydroclimate variability and phytoplankton responses

The observed phytoplankton changes closely covaried with the long-term weather conditions in the southwestern Mediterranean Sea that have displayed a conspicuous SST increase (Giorgi, 2006; Macias et al.,

2013). Moreover, rising chlorophyll concentrations in summer suggest: (i) that nutrient limitation via stratification unlikely drive the phytoplankton seasonal cycle in this shallow and eutrophic area (Sommer et al., 2012) and (ii) an increasing resource availability or nutrient supply (sensu Marañon et al., 2015). This shallow area is affected, via precipitation, by highly eutrophic systems such as coastal lagoons, small rivers and harbors receiving anthropic nutrient loads from sewage and

fertilizers used in agriculture (Souissi et al., 2000). Our analysis brings quantitative analysis of these processes, describing a threshold of precipitation that lead on high chlorophyll levels as a proxy of eutrophic conditions here (approx.  $2 \text{ kg m}^{-2} \text{ d}^{-1}$ , Fig. SI 4).

The changing environmental conditions yielded a shift from an initial dominance of microphytoplankton or large cells ( $>20 \mu\text{m}$ ) before the early 2000s to a final dominance of nanophytoplankton ( $2\text{--}20 \mu\text{m}$ ) after 2003. Nanophytoplankton fall within the medium size range that dominates the unimodal size-growth curve for phytoplankton, where several bloom-forming species are represented (Marañón et al., 2013). Small cells may outcompete large cells under increasing and less intermittent nutrient inputs, mainly due to the higher growth rates, although their storage capacity is lower. For instance, we noticed a succession towards smaller diatoms, such as *Phaeodactylum tricorutum*, which falls in the intermediate sizes presenting high growth rates (Marañón et al., 2013) (see Fig. 3). Theoretical work has shown that higher and constant nutrient alters the dynamics of diatoms size structure promoting a shift towards a dominance of smaller diatoms (Litchman et al., 2009). In line with this, recent works emphasise the overlooked role of small diatoms, being occasionally major contributors within phytoplankton blooms and carbon export in nutrient-rich and turbulent marine ecosystems (Leblanc et al., 2018).

Regarding the rising abundance of cyanobacteria, an increasing presence of this group has been related to warmer and eutrophic conditions (Paerl and Paul, 2012). Cyanobacteria proliferations have been shown favored by higher temperatures (often above  $25 \text{ }^\circ\text{C}$ ) and nutrient loads, where they grow better than do other phytoplankton species, such as diatoms and green algae (Paerl and Huisman, 2008). We refer here the cyanobacteria that fall within nano-size range, but no other smaller within picophytoplankton, as *Synechococcus* and *Prochlorococcus* sp., which play a key role in oligotrophic open sea ecosystems (Platt and Li, 1986).

#### 4.2. Biodiversity, ecosystem functioning and food web response

The conspicuous loss of diversity shown in the phytoplankton community is in agreement with the reported global trend of marine biodiversity losses (Sala and Knowlton, 2006) (Figs. 2 c and 3). Such diversity decline warns on wide consequences at several scales, as diversity stabilize resource use efficiency and overall the aquatic ecosystem functioning (Ptacnik et al., 2008). In species-poor communities, resources use is less efficient, which promotes available niche-space situations that may favor species invasion or resource monopolization, such as the *P. tricorutum* blooms we observed during the last years of the period investigated (Figs. 2 and 3). Overall, these processes within less diverse communities, point to a reduced stability and predictability of the ecosystem.

Regarding the potential contribution of top down control, with the caveat that no quantitative zooplankton data was available, it is worth noticing that gelatinous zooplankton have significantly increased in the Western Mediterranean over the last decades (Licandro et al., 2010; Molinero et al., 2008). Particularly in the Gulf of Tunis, mild winters has been related with optimal conditions favoring *Pelagia noctiluca* reproduction and outbreaks (Daly Yahia et al., 2010). This scyphozoan jellyfish could promote trophic cascades derived from their high predation capacity (Acuña et al., 2011; Brotz et al., 2012; Tiselius and Møller, 2017). Jellyfish diet consists mainly of copepods, but also meroplankton, ichthyoplankton and other gelatinous zooplankton (Purcell et al., 2014). However contrarily to the observed pattern, larger abundances of these voracious predators may foster microphytoplankton growth by reducing copepods biomass (Stibor et al., 2004; Tiselius and Møller, 2017). Hence, we suggest that the top down control by copepods did not play a leading role in the observed phytoplankton changes, instead we hypothesize a bottom up control driving the observed response of the phytoplankton community, e.g. such as resources supply increase in this period. Moreover, these structural changes in the

phytoplankton community, e.g. shift in the mean community size, along with larger abundances of jellyfish might further affect food web carbon pathways and permeate the entire food web.

#### 4.3. Insights for mediterranean ecosystems in the next future

A concomitant warming with shrinking phytoplankton sizes has been reported in northern Mediterranean regions (Marty et al., 2002; Mozetič et al., 2012, 2010; Zingone et al., 2019). Nevertheless, the suggested driving mechanisms of such patterns point out a leading role of an increasing stratification, as the main driver of the mixed layer dynamics and resources availability for phytoplankton. We emphasise that in neritic ecosystems, such as the coastal sites we investigated, local or regional factors could drive the environmental conditions or resource availability, leading on different responses of the phytoplankton communities. For instance, a positive trend was recently registered in chlorophyll from satellite data around the Nile Delta, also in the southern Mediterranean coast (Lazzari et al., 2012), whereas a decrease in nutrient inputs and eutrophic conditions in the Po delta (North Adriatic Sea) did not show a significant link with the trend in phytoplankton size changes (Aubry et al., 2012).

Climate projections for the Mediterranean Sea warns on a warming trend along with a decline in precipitation and more frequent extreme events (see Fig. 1 b,d) (Alpert et al., 2002; Hertig and Jacobeit, 2008). This scenario suggests modifications in the amount and frequency of the natural nutrient supply that might foster changes in the phytoplankton community (Litchman et al., 2009; Macias et al., 2010). It is worth noticing however that anthropogenic nutrient loads could mask all these processes. As described in previous works, the Mediterranean “tropicalization” threatens this diversity hotspot (Bianchi, 2007; Vergés et al., 2014). This phenomenon is not only supported by warmer and/or more oligotrophic conditions as formerly described, it also depend on local factors, i.e. riverine and/or anthropogenic inputs, that may open ecological niches for tropical invasive species from eutrophic systems, which may be introduced in the Mediterranean Sea via ballast waters (Coll et al., 2010).

The analysis of long-term field data sheds light on pelagic ecosystem responses to warming conditions. Phytoplankton communities are adapted to local temperatures (Thomas et al., 2012), while optimum temperatures of locally adapted phytoplankton are higher than the annual mean temperature they experience, and therefore the warmer the local mean temperature the closer is to species optimum. This is not trivial if we consider the negative skewness of the thermal tolerance curve, which suggests that the phytoplankton growth response to variations in temperature may be more sensitive to warming than cooling conditions. Therefore, subtropical communities are more vulnerable to warming, which may foster losses in diversity, as recently predicted by global synthesis on the phytoplankton-temperature interactions (Thomas et al., 2012). During the sampled period the annual mean temperature raised approx.  $1 \text{ }^\circ\text{C}$ , while a sustained increase is expected in the next century, particularly during summer months (approx.  $1.5\text{--}2 \text{ }^\circ\text{C}$ ) (Gualdi et al., 2013; Shaltout and Omstedt, 2014). This warns on drastic changes phytoplankton diversity, likely shifting towards a more tropical community (Thomas et al., 2012).

## 5. Conclusions

Our results show conspicuous shifts in the structure of phytoplankton communities likely fostered by the compound effects of rising precipitation and temperatures experienced in the Bay of Tunis during the last decades. The observed changes in the structure of phytoplankton community suggest a reorganization in the plankton food web. Hence, southern Mediterranean warming projections, together with anthropogenic nutrient inputs warn on the high vulnerability these ecosystems experience to invasions, but also substantial changes in the phytoplankton diversity and size structure, which ultimately will yield to a

less predictable and stable system.

### Author contributions

We state the manuscript is original and is not submitted elsewhere. All the listed authors are in agreement and approve the submitted version. NS, OK-DY and MNDY led the sampling and field data analysis. E R-R, JCM and US conceived this study and performed the statistical analysis of the results. All the authors contributed during the writing and revision of the manuscript.

### Declaration of competing interest

None.

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### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecss.2019.106574>.

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